Seasonal Colonization and Decomposition of Rat Carrion in Water and on Land in an Open Field in South Carolina

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ABSTRACT Decomposition and insect colonization of rat, *Rattus rattus* L., carrion on land and in water were compared during summer and winter in a plowed field in northwestern South Carolina. During winter, carcasses on land reached the dried-remains stage of decomposition, whereas carcasses in water reached the early-floating stage. During summer, carcasses in both habitats entered the final-remains stage of decomposition in 1–2 wk. Fewer than 30 species of carrion insects were recorded from the carcasses over the duration of the study, probably reflecting the small size of the carcasses and the depauperate fauna of the habitat. Three species of blow flies—*Cynomyopsis cadaverina* (Robineau-Desvoidy), *Calliphora vicina* Robineau-Desvoidy, and *Lucilia illustris* (Meigen)—colonized carrion on land during winter, but no insects colonized carrion in water during winter. Two species of blow flies, *Cochliomyia macellaria* (F.) and *Phaenicia sericata* (Meigen), and 1 species of flesh fly, *Sarcophaga bullata* Parker, colonized the carrion on land and in water during summer; the blow fly, *Phormia regina* (Meigen), colonized only the carrion on land. This study demonstrated seasonal variation in decomposition and colonization patterns of carrion in contrasting habitats, with important implications for forensic entomology.

KEY WORDS carrion, decomposition, Calliphoridae, forensic entomology

THE LARGE BODY of literature on arthropod colonization of terrestrial carrion has great utility for forensic entomology (e.g., Smith 1986, Catts and Goff 1992). However, little is known about this colonization process in water. Some of the earliest research on arthropods of carrion in aquatic systems was conducted by Payne (1967), who documented arthropods on pig carcasses in water-filled tanks. Singh and Greenberg (1994) examined the effects of submersion on the survival of calliphorid pupae. Other workers have documented aquatic insects on carrion (Brusven and Scoggan 1969, Hawley et al. 1989, Schuldt and Hershey 1995, Vance et al. 1995) and noted their usefulness in forensic entomology (Haskell et al. 1989, Keiper et al. 1997).

Because most research on arthropods of carrion has been conducted during the warm months of the year (e.g., Payne 1967, Tessmer and Meek 1996), winter colonization has been studied inadequately. The few available winter studies have examined colonization of dog carrion in Tennessee (Reed 1958) and blow fly activity on carrion in the southwestern United States (Deonier 1940). In addition, a nitidulid beetle was reported from a human corpse in winter in Colorado (Adair and Kondratieff 1996).

The current study examines insect colonization and rates of decay of rat carcasses on land and in water during summer and winter in upstate South Carolina, the same area where Payne (1963, 1965, 1967) conducted his pioneering research on pig carrion more than 30 yr earlier. Our study compares colonization and decomposition of carrion in water and on land, and examines arthropod colonization of carrion in water during the winter.

Materials and Methods

Experiments were conducted in Clemson, South Carolina (34° 40′ N, 82° 50′ W) in a plot (12 by 52 m) surrounded by local grasses and weeds. A hardwood forest was located ≈300 m to the east. The plot was plowed 14–21 d before each experiment to create a homogeneous habitat.

Two experiments were conducted during winter (5 January–29 March 1995, 12 January–4 April 1996) and 2 in summer (18 July–2 August 1995, 17 August–1 September 1995). In each experiment, 30 white rats (*Rattus rattus* L., 1–2 yr old, 0.25–0.75 kg) were euthanized by oxygen deprivation 1 h before the experiment. Carcasses were placed in green plastic tubs (60.9 by 40.6 by 22.2 cm) with their upper rims flush with the ground surface. Each pair of containers (1 dry, 1 maintained with 35 liters of water) was placed randomly along a north–south axis, with the east–west position determined randomly. The experiment design allowed the influence of water to be isolated. Each

Animal-use protocol 95-010 was approved by the Department of Research Services, Clemson University.

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Table 1. Mean ± SD number of dipteran immatures taken from rat carcasses on land in winter 1995 and 1996 in Clemson, SC, with respect to mean ± SD ambient and internal carcass temperatures and total rainfall (mm)

	C. cadaverina[a]	*C. vicina*[a]	*L. illustris*	Calliphorid eggs	Temp, °C				Rainfall
					Min.	Max	Midday	Carcass	
				Experiment 1 (1995)[b]					
25 Jan.	51.3 ± 15.1	11.3 ± 9.8	0.0	290.3 ± 275.1	2.1 ± 6.0	15.0 ± 3.9	7.3 ± 6.7	5.0 ± 6.0	79
15 Feb.	55.3 ± 21.6	126.3 ± 64.6	0.0	39.0 ± 35.1	−2.3 ± 5.4	7.6 ± 5.0	0.9 ± 4.5	2.5 ± 2.9	81
9 Mar.	52.7 ± 79.1	24.7 ± 31.5	0.0	23.3 ± 40.4	4.0 ± 5.0	14.6 ± 4.2	8.2 ± 4.8	10.0 ± 1.5	145
29 Mar.	2.0 ± 3.5	2.6 ± 3.8	27.7 ± 17.8	0.0	4.5 ± 4.2	21.0 ± 6.0	12.6 ± 8.0	7.7 ± 3.1	14
				Experiment 2 (1996)[b]					
1 Feb.	0.0	0.0	0.0	0.0	−2.1 ± 5.4	10.6 ± 4.0	NA	7.4 ± 1.3	111
22 Feb.	38.3 ± 41.9	0.0	0.0	254.3 ± 340.4	0.6 ± 6.6	10.7 ± 6.0	13.6 ± 6.4	8.7 ± 6.5	60
13 Mar.	42.7 ± 58.3	2.0 ± 3.5	0.0	28.0 ± 45.1	2.6 ± 7.0	17.4 ± 5.7	15.7 ± 7.6	16.1 ± 7.1	120
4 April	0.0	0.0	0.0	0.0	4.9 ± 4.5	16.3 ± 6.3	14.2 ± 6.6	17.1 ± 7.3	38

NA, not available.
[a] Numbers are based on identifications of reared adults; all other larval numbers are based on identifications of larvae and reared adults.
[b] Carcasses were placed in the field on 5 January (experiment 1) and 12 January (experiment 2).

dry tub had a 1.3-cm^2 hole covered with 1.5-mm^2 nylon mesh on the bottom edge for drainage. Tubs with water had similar holes 2.5 cm below their rims for drainage. One rat was placed in each container. Scavengers were excluded with polycoated 2.5-cm mesh hexnetting secured with metal stakes.

The external appearance of each carcass was recorded daily. Three pairs of rats were removed randomly from the field every 20–22 d in winter and every 3–4 d in summer. Each rat was photographed and its physical condition recorded. A ventral incision was made from the anus to the lower mandible and a 2nd incision was made through the sternum; the extent of internal decay was recorded. Samples of eggs and larvae were removed from the carcasses and reared (24–27°C, 75–85% RH, and a photoperiod of 12:12 h) to adults on 10–20 g of beef liver in 30-ml plastic cups (15–25 eggs or early instars per cup, reduced to 5 per cup with fresh liver for 3rd instars). All remaining arthropods were removed by hand from the carcasses and tubs and preserved in 80% ethanol. Arthropods that fell into the traps but are not associated with carrion ecology were omitted from the study. Voucher specimens of carrion insects were deposited in the Clemson University Arthropod Collection or the Cornell University Insect Collection, Ithaca, NY.

In the 1995 winter experiment, internal temperatures were monitored in 12 pairs of rats that were divided randomly into 4 groups of 3 pairs each. Every 3 d, internal temperatures of 1 group were measured by inserting a digital thermometer (Taylor model no. 9850) into the body cavity via the anus. In subsequent experiments, daily internal temperatures were measured with a digital Fisherbrand Water Resistant Thermometer (Control Company, Friendswood, TX) inserted permanently, via the anus, into the body cavity of 3 pairs of rats. The following environmental conditions were recorded daily (≈1200 hours) at ground level: midday, minimum, and maximum ambient temperatures (maximum-minimum thermometer, shaded); water temperature (hand-held thermometer, shaded); and precipitation (rain gauge).

Results

Colonization of Carcasses on Land. During winter, 16 carrion-associated insect species were recovered from carcasses on land, whereas 5 were recovered during summer. The 3 species of calliphorids colonizing the winter carcasses were, in descending order of abundance, *Cynomyopsis cadaverina* (Robineau-Desvoidy), *Calliphora vicina* Robineau-Desvoidy, and *Lucilia illustris* (Meigen) (Table 1). *C. cadaverina* colonized the carcasses first, followed by *C. vicina,* and finally *L. illustris.* During summer, the 3 species of calliphorids and 1 species of sarcophagid colonizing the carcasses were, in descending order, *Cochliomyia macellaria* (F.), *Phaenicia sericata* (Meigen), *Sarcophaga bullata* Parker, and *Phormia regina* (Meigen) (Table 2). *C. macellaria* was the most abundant insect colonizing rat carrion. The chalcidid wasp, *Brachymeria fonscolmbei* Defour, parasitized larvae of *S. bullata* from rats on land.

During winter and summer, calliphorids oviposited in crevices between limbs and the body and in natural orifices, such as the mouth and anus. The mean number of eggs in the 1st sample of the 1st winter experiment was 290 per carcass, decreasing to 0 in the remaining samples (Table 1). In the 2nd winter experiment, no colonization occurred during the first 20 d, but thereafter the trend was similar, with a mean of 254 eggs per carcass, decreasing to 0 in the final sample. In the 1st summer samples, means of 628 and 2,550 eggs per carcass were recorded (Table 2). Eggs were not found on the carcasses in subsequent samples.

The major sites of larval concentration (>60% of larvae per sample) progressed from natural body openings to the center of the body. In the 1st sample, larvae were concentrated around the mouth and anus, whereas in the 2nd sample, larvae were present on the neck and lower abdomen. In the 3rd sample, they were in the abdominal and cardiac regions; however, in the 4th sample, they were concentrated in the limbs.

From 1 to 6 adults of each of the following staphylinid beetles were found on carcasses on land

Table 2. Mean ± SD number of dipteran immatures taken from rat carcasses on land in summer 1995 in Clemson, SC, with respect to mean ± SD ambient and internal carcass temperatures and total rainfall (mm)

	C. macellaria	*P. sericata*	*P. regina*	*S. bullata*	Calliphorid eggs	Temp, °C				Rainfall
						Min.	Max	Midday	Carcass	
					Experiment 1[a]					
21 July	907.6 ± 1067.4	463.3 ± 516.4	400.7 ± 693.9	627.3 ± 939.5	628.0 ± 905.4	22.8 ± 0.6	33.6 ± 1.6	33.6 ± 1.4	46.8 ± 4.1	0
25 July	228.6 ± 362.8	0.3 ± 0.6	0.3 ± 0.6	33.2 ± 49.1[b]	0.0	22.3 ± 1.0	34.9 ± 1.8	34.9 ± 1.4	45.5 ± 12.3	0
29 July	0.0	0.0	0.0	0.0	0.0	22.0 ± 0.1	33.7 ± 2.6	33.7 ± 2.5	42.4 ± 10.7	28
2 Aug.	0.0	0.0	0.0	0.0	0.0	20.8 ± 0.5	32.3 ± 0.9	32.9 ± 0.6	32.5 ± 4.7	0
					Experiment 2[a]					
20 Aug.	2,248.0 ± 2,344.5	916.3 ± 695.4	0.0	117.3 ± 203.2	2,550.3 ± 4,228.9	23.1 ± 2.2	34.0 ± 2.5	30.7 ± 5.0	41.6 ± 7.8	23
24 Aug.	1,490.0 ± 2,580.7	218.3 ± 378.2	0.0	14.3 ± 13.2	0.0	21.6 ± 0.6	30.2 ± 2.6	27.8 ± 4.7	30.4 ± 4.2	85
28 Aug.	0.0	0.0	0.0	0.0	0.0	21.1 ± 0.0	29.0 ± 1.6	NA	NA	123
1 Sept.	0.0	0.0	0.0	0.0	0.0	20.0 ± 0.0	31.1 ± 1.6	NA	NA	0

NA, not available.
[a] Carcasses were placed in the field on 18 July (experiment 1) and 17 August (experiment 2).
[b] Nine adults of *Brachymeria fonscolmbei* (Hymenoptera: Chalcididae) were reared from this sample.

during winter: *Achenomorphus corticinus* (Gravenhorst), *Aleochara lata* Gravenhorst, *Aleochara notula* Erichson, *Aleochara verna* Say, *Aleochara* sp., *Anotylus* sp., *Bisnius inquietus* (Erichson), *Creophilus maxillosus* (L.), *Neohypnus* sp., *Omalium* sp., *Tachinus axillaris* Erichson, undetermined Athetini, and undetermined Paederinae. During summer, 2 adults of the staphylinid *Platydracus maculosus* (Gravenhorst) were taken from carcasses on land.

Colonization of Carcasses in Water. No Diptera colonized carcasses in water during winter. However, 7 staphylinids of 6 species were found floating in the water: *A. verna, B. inquietus, C. maxillosus, Mycetoporus lucidulus* LeConte, *Omalium* sp., and ?*Oxypoda* sp.

During summer, 11 carrion-associated, terrestrial species were collected from the carcasses. In the 1st summer experiment, only *S. bullata* colonized exposed areas of the floating carrion, whereas *C. macellaria, P. sericata,* and *S. bullata* colonized floating carrion in the 2nd experiment (Table 3). Calliphorid eggs collected from carcass hair averaged 8,632 (range, 368–24,454) per carcass in the 1st sample and 161 per carcass in the 2nd sample.

The heteropteran, *Alydus eurinus* (Say), fed on exposed regions of the carrion during summer (mean ± SD = 1.3 ± 2.3 per carcass). Nine staphylinids of 5 species (*A. notula, Anotylus* sp., *Gabronthus mgogoricus* Tottenham, *P. maculosus,* and *Tinotus* sp.) were recovered from floating carcasses in summer, plus single adults of the silphid beetle *Necrophila americana* (L.) and the dermestid beetle *Dermestes caninus* Germar. Aquatic taxa that were collected and might have fed on the carcasses included early instars of the dipteran families Chironomidae (*Chironomus* sp.), Ephydridae, and Psychodidae. A mean of ≤12 larvae per tub was present on each sampling date, with the exception of Psychodidae (57.5 ± 13.2) in sample 2 and Ephydridae (335.0 ± 580.2) in sample 4 of the 2nd experiment.

Decomposition of Carcasses on Land. Seven to 29 d into the winter experiments, bloating was detected in the abdomen. As carcasses expanded, adult calliphorid activity increased from 2–3 to 10–15 per carcass. First instars appeared in natural orifices of the body after 13 (1995) to 41 d (1996). By the end of the experiments, the hind torso and head were cleared completely of soft tissues and the gastric system had turned black. Larvae (86% *L. illustris*) remaining on day 80 fed on limb tissues.

Table 3. Mean ± SD number of dipteran immatures taken from rat carcasses in water in summer 1995 in Clemson, SC, with respect to mean ± SD water and internal carcass temperatures and total rainfall (mm)

	C. macellaria	*P. sericata*	*S. bullata*	Calliphorid eggs	Water temp, °C[a]	Carcass temp, °C
			Experiment 1[b]			
21 July	0.0	0.0	0.0	0.0	28.8 ± 9.9	34.1 ± 1.6
25 July	0.0	0.0	64.0 ± 104.8	0.0	34.0 ± 2.8	33.7 ± 3.8
29 July	0.0	0.0	4.3 ± 7.5	0.0	32.6 ± 4.1	37.8 ± 8.8
2 Aug.	0.0	0.0	0.0	0.0	31.9 ± 4.9	33.4 ± 4.5
			Experiment 2[b]			
20 Aug.	1,318.3 ± 1,307.3	0.0	31.3 ± 54.3	8,632.0 ± 13,706.8	33.5 ± 5.5	33.4 ± 5.1
24 Aug.	4.7 ± 5.7	25.3 ± 29.7	14.7 ± 18.9	161.3 ± 253.0	29.5 ± 5.8	29.9 ± 6.3
28 Aug.	0.0	0.0	0.0	0.0	NA	NA
1 Sept.	0.0	0.0	0.0	0.0	NA	NA

NA, not available.
[a] Minimum, maximum, and midday ambient temperatures are provided in Table 2.
[b] Carcasses were placed in the field on 18 July (experiment 1) and 17 August (experiment 2).

During summer, bloating was apparent after 1 d, and calliphorid eggs were present in natural orifices and crevices of the body. On day 3, first-instar calliphorids and sarcophagids appeared in body orifices. Abdomens of carcasses on land ruptured on day 3 of the 2nd summer experiment, exposing the internal organs. By the 5th day of both experiments, the head and neck had been cleared of soft tissues, exposing the bones; larvae were present in the abdominal and cardiac regions. On the 7th d, larval Diptera began migrating from the carcasses. About 85 mm of rain occurred on days 4–7 in the 2nd summer experiment, and dead larvae were found in 2 carcasses. No larvae were collected from the carcasses during the "dried-remains" stage, which began on day 6–7 and lasted until the experiments terminated on day 16, although dermestid beetles (*D. caninus*) occurred beneath the carcasses.

During winter, internal carcass temperatures (1st and 2nd experiments, respectively; Table 1) were correlated ($P \leq 0.01$) with maximum ($r = 0.59$, df = 18; $r = 0.69$, df = 69), minimum ($r = 0.78$, df = 18; $r = 0.46$, df = 69), and midday ($r = 0.79$, df = 16; $r = 0.47$, df = 35) ambient temperatures. During summer, the internal temperature of carcasses on land was correlated significantly only with midday ambient temperature in the 2nd experiment ($r = 0.88$, $P \leq 0.05$, df = 3); sample sizes were limited because thermometers fell from carcasses after extensive decomposition. The highest recorded internal temperature was 60.5°C, which was 29.5°C above ambient temperature (28 July).

Decomposition of Carcasses in Water. Carcasses of the 1st winter experiment began to float after 46 d. Externally, the carcasses became covered by algae (*Protococcus* sp.), and hair fell from the exposed regions, which became dry and tanned. After 80 d, internal decay was negligible. In the 2nd winter experiment, carcasses began to float after 44 d, then submerged again after 15 d, and eventually decomposed internally without the presence of insects.

During summer, carcasses in the 1st experiment sank when placed in the water, whereas carcasses of the 2nd experiment remained afloat. After 18 h, the carcasses in the 1st experiment rose to the surface, exposing the abdomen. On day 4 of the 2nd experiment, calliphorid eggs appeared on hair of the exposed regions and by day 5, first instars appeared. In both experiments, hair fell from the body which, along the water's edge, was covered by algae (*Protococcus*). By day 7, holes (2.5 cm diameter) in exposed regions of the bloated carcasses contained larvae. Carcasses began to sink by the 8th day, and dead larvae appeared on the water surface. By day 12, the hind torsos had been cleared of soft tissues and internal organs had disappeared. On day 16, skeletons lay on the bottoms of the tubs.

Internal temperatures of carcasses in water during winter experiments (1st and 2nd, respectively) were correlated ($P \leq 0.01$, except as otherwise given) with ambient maximum air ($r = 0.64$, df = 18; $r = 0.69$, df = 69), minimum air ($r = 0.51$, $P \leq 0.05$, df = 18; $r = 0.59$, df = 69), midday air ($r = 0.74$, df = 16; $r = 0.62$, df = 35), and midday water ($r = 0.99$, df = 11; $r = 0.60$, df = 61) temperatures. Ice ($\leq$2.5 cm) formed on the surface of the water for 7 d during the 1st experiment and 1 d during the 2nd experiment. Internal temperatures of carcasses in water, during the 2nd summer experiment, were correlated significantly with ambient maximum air ($r = 0.94$, $P \leq 0.05$, df = 3), midday air ($r = 0.91$, $P \leq 0.05$, df = 3), and water ($r = 0.99$, $P \leq 0.01$, df = 3) temperatures; however, sample sizes were small because extensive decomposition caused the thermometers to fall out of the carcasses. Correlations were not significant ($P > 0.05$) during the 2nd summer experiment. The highest internal temperature for a carcass in water was 48.0°C, 15.8°C above ambient air temperature.

Developmental Rates of Calliphorids. *C. cadaverina* and *C. vicina* required a mean of 15.8 ± 0.89 d ($n = 51$) and 18.1 ± 1.60 d ($n = 15$), respectively, to complete development from 1st instar to adult in the laboratory (24–27°C); *C. cadaverina* completed development significantly faster ($t = -5.36$, $P \leq 0.0001$, df = 16) than *C. vicina*. *C. macellaria* required 15.0 ± 0.00 d ($n = 31$) to complete development from egg to adult in the laboratory (24–27°C).

Discussion

The stages of decomposition of rat carcasses on land during winter and summer and in water during summer were similar to those observed for fetal pig carrion by Payne (1967). However, carcasses in water during winter did not decompose according to Payne's (1967) stages, which are based largely on summer decomposition through terrestrial insect colonization. Decomposition can also be accomplished by anaerobic bacteria in the gut (Weigelt 1989) and, in natural bodies of water, aquatic organisms aid decomposition (Keiper et al. 1997).

Rates of decomposition vary with temperature (Deonier 1940), which affects bacterial activity (Swift et al. 1979) and developmental rates of carrion-frequenting insects (Ash and Greenberg 1975). Carcasses on land in our study reached the advanced stage of decay 10–15 times faster, and carcasses in water reached the early floating stage more than 40 times faster during summer than during winter. In summer, carcasses on land decomposed within a week, or about twice as fast as carcasses in water, leaving only hair, cartilage, and bones. Similarly, 90% decomposition of fetal pigs on land occurred in 6 d in the same geographic area (Payne 1967). Terrestrial decomposition of the soft tissues of pig carrion required 10–23 d in Hawaii (Tullis and Goff 1987).

The greatest differences between carcasses on land and ambient temperature and between carcasses in water and ambient temperature were 29.5 and 15.8°C, respectively. Because larvae are able to increase the temperature of their microhabitat (Deonier 1940, Greenberg 1991), the reduced insect colonization of the carrion in water probably generated less heat. Water also might have provided a thermal buffer. However, a small tub of water in a plowed field would

be influenced by solar radiation more than would larger bodies of water, necessitating caution when extrapolating these results to other aquatic environments.

Water prevented colonization by terrestrial insects during winter because the carcasses remained below the surface for more than 6 wk. Because bacterial metabolic activity is sensitive to temperature (Swift et al. 1979), the rate of gas production is greater during warm weather, causing the carcasses to rise sooner, thereby exposing them to terrestrial arthropods sooner than during winter. Even in natural aquatic habitats, where submerged carcasses are available for colonization by aquatic arthropods, cold temperatures can slow the decomposition process (Keiper et al. 1997). During summer, carcasses in water were colonized 2–4 h after the abdominal area became exposed to air, but the number of colonizing insects generally was less than on the carcasses on land, possibly because less surface area was available for colonization. Limited or excessive moisture and precipitation may also prevent or delay insect colonization and development (Graham-Smith 1937, Payne 1967).

The number of species (<30) colonizing the rat carrion was far less than that reported in other studies (Payne 1967, Goff et al. 1986, Tantawi et al. 1996), not only because the carcasses were small, but perhaps also because the habitat—an exposed, plowed field—had a depauperate faunal pool. Few carrion studies or forensic investigations have been conducted in open, agricultural settings; our results indicate that no species were unique to this habitat, although species richness was limited. Species composition and succession were generally consistent among carcasses within each season and habitat. However, the number of calliphorid eggs varied as much as 66-fold in carcasses only 11 m apart, emphasizing the need for replication. *C. cadaverina* and *C. vicina* were primary colonizers from January to mid-March, and *L. illustris* was the primary colonizer in late March. Hall (1948) described all 3 as early-spring species. *C. macellaria* was the principal colonizer of carrion during July and August, in agreement with other studies in the southeastern states (Payne 1967, Tessmer and Meek 1996); it also has been collected during winter in coastal South Carolina (Hall 1948). Our laboratory development times for *C. cadaverina* and *C. vicina* correspond with those of previous studies (Kamal 1958), but our development times for *C. macellaria* are ≈1.5–2.0 times longer than those recorded by Byrd and Butler (1996), possibly because the latter authors reared larvae in large groups and sampled only the largest larvae.

We conclude that habitat and season influence decomposition and insect colonization of carrion. In forensic investigations, these findings can aid in determining the time of year that death might have occurred (Catts and Goff 1992). Our study was designed to isolate the influence of water on decomposition and colonization. By using artificial containers, we excluded aquatic arthropods during winter and minimized their colonization during summer. Further investigation is now required to determine the role of aquatic arthropods in the decomposition process in natural aquatic habitats.

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References Cited

Adair, T. W., and B. C. Kondratieff. 1996. The occurrence of *Nitidula flavomaculata* (Coleoptera: Nitidulidae) on a human corpse. Entomol. News 107: 233–236.

Ash, N., and B. Greenberg. 1975. Developmental temperature responses of the sibling species *Phaenicia sericata* and *Phaenicia pallescens*. Ann. Entomol. Soc. Am. 68: 197–200.

Brusven, M. A., and A. C. Scoggan. 1969. Sarcophagous habits of Trichoptera larvae on dead fish. Entomol. News 80: 103–105.

Byrd, J. H., and J. F. Butler. 1996. Effects of temperature on *Cochliomyia macellaria* (Diptera: Calliphoridae) development. J. Med. Entomol. 33: 901–905.

Catts, E. P., and M. L. Goff. 1992. Forensic entomology in criminal investigations. Annu. Rev. Entomol. 37: 253–272.

Deonier, C. C. 1940. Carcass temperatures and their relation to winter blowfly populations and activity in the southwest. J. Econ. Entomol. 33: 166–170.

Goff, M. L., M. Early, C. B. Odom, and K. Tullis. 1986. A preliminary checklist of arthropods associated with exposed carrion in the Hawaiian Islands. Proc. Hawaii. Entomol. Soc. 26: 53–57.

Graham-Smith, G. S. 1937. Observations on the habits and parasites of common flies. Parasitology 8: 441–542.

Greenberg, B. 1991. Flies as forensic indicators. J. Med. Entomol. 28: 565–577.

Hall, D. G. 1948. The blowflies of North America. Thomas Say Foundation Monographs, vol. 4. Entomological Society of America, Lanham, MD.

Haskell, N. H., D. G. McShaffrey, D. A. Hawley, R. E. Williams, and J. E. Pless. 1989. Use of aquatic insects in determining submersion interval. J. Forensic Sci. 34: 622–632.

Hawley, D. A., N. H. Haskell, D. G. McShaffrey, R. E. Williams, and J. E. Pless. 1989. Identification of a red "fiber": Chironomid larvae. J. Forensic Sci. 34: 617–621.

Kamal, A. S. 1958. Comparative study of thirteen species of sarcosaprophagous Calliphoridae and Sarcophagidae (Diptera) I. Bionomics. Ann. Entomol. Soc. Am. 51: 261–271.

Keiper, J. B., E. G. Chapman, and B. A. Foote. 1997. Midge larvae (Diptera: Chironomidae) as indicators of postmortem submersion interval of carcasses in a woodland stream: a preliminary report. J. Forensic Sci. 42: 1074–1079.

Payne, J. A. 1963. A summer carrion study of the baby pig, *Sus scrofa,* Linnaeus. M.S. thesis, Clemson University, Clemson, SC.

1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology 46: 592-602.

1967. A comparative ecological study of pig carrion decomposition and animal succession with special reference to the insects. Ph.D. dissertation, Clemson University, Clemson, SC.

Reed, H. B., Jr. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. Am. Midl. Nat. 59: 213-245.

Schuldt, J. A., and A. E. Hershey. 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. J. North Am. Benthol. Soc. 14: 259-268.

Singh, D., and B. Greenberg. 1994. Survival after submergence in the pupae of five species of blow flies (Diptera: Calliphoridae). J. Med. Entomol. 31: 757-759.

Smith, K.G.V. 1986. A manual of forensic entomology. British Museum (Natural History), London, and Cornell University Press, Ithaca, NY.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Tantawi, T. I., E. M. El-Kady, B. Greenberg, and H. A. El-Ghaffar. 1996. Arthropod succession on exposed rabbit carrion in Alexandria, Egypt. J. Med. Entomol. 33: 566-580.

Tessmer, J. W., and C. L. Meek. 1996. Dispersal and distribution of Calliphoridae (Diptera) immatures from animal carcasses in southern Louisiana. J. Med. Entomol. 33: 665-669.

Tullis, K., and M. L. Goff. 1987. Arthropod succession in exposed carrion in a tropical rainforest on Oahu Island, Hawaii. J. Med. Entomol. 24: 332-339.

Vance, G. M., J. K. VanDyk, and W. A. Rowley. 1995. A device for sampling aquatic insects associated with carrion in water. J. Forensic Sci. 40: 479-482.

Weigelt, J. 1989. Recent vertebrate carcasses and their paleobiological implications. University of Chicago Press, Chicago, IL.

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